Geographic Variation of *Bufo spinulosus* in Chile

Jose M. Cei

Introduction

Bufo spinulosus Wiegmann occupies an extensive area reaching from the northern Andean highlands of Peru to the cold southern rainforests of Chile (Province of Chiloe). On the western slopes of the Cordillera, it is found from an elevation of 4,500 meters to the seashore. On the eastern slopes of the Andes, it is only found above 1,200 meters. In Chile this toad is the most adaptive and predominant form, inhabiting almost all of the possible ecological niches. Five well-defined geographical forms were recognized by Vellard (1959) in Peru. The description and interrelation of the numerous Chilean populations of this polymorphic toad and their geographical distribution is the purpose of the present paper.

Material and Methods

All of the studied samples were observed and measured alive in the field in 1957, with the exception of Valdivian specimens collected in 1952 and preserved in a mixture of alcohol and formalin. Color descriptions are based entirely on living specimens. The characters analyzed are those appearing in the generally accepted diagnoses of the species (Wiegmann, 1834; Boulenger, 1882). Sexual maturity was determined according to the criteria cited by Inger (1954:203). Measurements were taken with calipers and are accurate to 0.5 mm. The standard error was calculated for the various measurements, and the Student's t test and the tables of Fisher and Yates (1948) were used.

The following measurements were made: snout-vent length; head width taken between centers of tympana; head length from tip of snout to line joining centers of tympana; hind leg length from tip of fourth toe to groin; fore leg length, from tip of third finger to axilla; distance from tip of snout to nostril; distance from nostril to eye; interorbital width; width of upper eyelid; snout length, from tip of snout to interorbital axis; parotoid diameter.

Samples were examined from the following localities (Fig. 1):

1. Puna de Atacama, E. of San Pedro de Atacama, Prov. of Antofagasta; under stones and rocks, along the little streams of the mountains (Arroyo Bilema) above 2500 meters (July, 1957): *19*[1], *413*, *414* (Fig. 2).
2. Paposo (Quebrada de Caleta Paposo). Prov. of Antofagasta; under stones and in water, in little streams, near the Pacific

[1]Italicized numbers refer to collections of the Centro Investigaciones Zoologicas (C.I.Z.) of the University of Chile, Santiago, in which some samples are deposited.

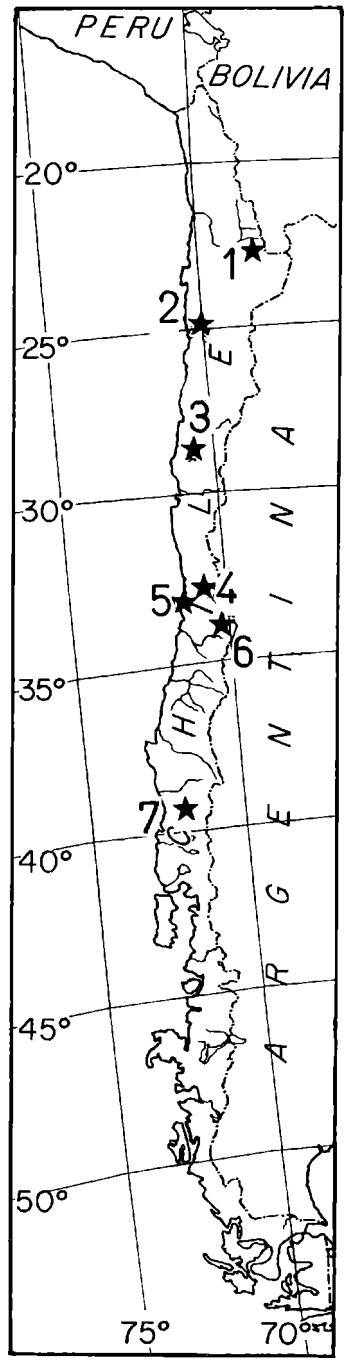

Fig. 1. Map of Chile showing the seven populations studied: 1. Puna de Atacama, 2. Paposo, 3. Vallenar, 4. Santiago de Chile, 5. Casablanca, 6. Central Cordillera, 7. Valdivian Lakes.

Coast, a few hundred meters above sea level (July, 1957): *18.*

3. Vallenar, Prov. of Atacama; under stones in Huasco River, near the town, 380 meters (July, 1957): *131,* (Fig. 2).
4. Santiago de Chile, Potrerillo, near Nilhué Bridge, 800 meters (September, 1957).
5. Casablanca, Curacaví Valley, S. E. of Valparaiso, arid coast zone, 300 meters (Aug., 1957).
6. Central Cordilleras, E. of Santiago, lo Valdés, above 1500 meters (Sept., 1957): *415,* (Fig. 2).
7. Valdivian Lakes, Prov. of Valdivia, near Enco and Caburgua (Summer, 1952): *54, 185,* (Fig. 2).

Of the 245 toads analyzed statistically, 106 were males, 88 females, and 51 unsexed juveniles. Observations made on 132 additional specimens from Chilean localities were not statistically considered: Putre, in Tarapacá mountains; Puna de Atacama; Loa River, N.W. of Calama; Copiapo, Prov. of Atacama; Talinay, Prov. of Coquimbo; Zapallar, N. of Valparaiso; Baño Morales, Central Cordilleras, Santiago, 2500 meters; Talca; Concepción; Angol. Prov. of Malleco; Valdivian Lakes.

Four geographic groups of Chilean populations are represented: (1) the toads from the northern arid mountains of Puna de Atacama; (2) the isolated populations of the rivers and streams of the Atacama Desert (Paposo and Vallenar); (3) the central Chilean populations of the xeric region of the *Acacia caven* steppe as far as the western Andean slope (Santiago, Casablanca, and Cordillera Central); and (4) the toads of the cold Valdivian rainforest of the extreme south. The ecological circumstances of each group are distinctive.

Analysis of Variation

Ranges and means and their standard errors of the eight measurements were calculated. Comparisons between each pair of samples were made for all eight measurements, considering sexes separately. In Table 1 statistically significant differences (P equal to or less than 0.05) are indicated by a plus sign, while a negative sign indicated comparisons that were not significantly different.

Sex dimorphism in the characters listed in Table 1 reached statistically significant levels in the Puna de Atacama sample (size, head shape, relative hind leg length, and nostril position), in the Cordillera Central sample (head shape and interorbital), and in the Valdivia sample (size).

Besides the characters listed in Table 1, the following also serve to distinguish the various populations:

1. When the hind limb is brought forward, the tibio-tarsal articulation usually (*i.e.,* 50 per cent or more of toads examined)

reaches the parotoids or beyond, but in 75 to 100 per cent of both sexes from Santiago and of females from Casablanca and Valdivia, that joint reaches only as far as the shoulder.

2. Very rough, warty skin characterizes toads from Puna de Atacama and the Cordillera Central, and both groups produce an irritating, sticky, and aromatic secretion. The skin in the remaining samples is relatively smooth (especially in Paposo-Vallenar toads) with rounded tubercles and produces very little secretion, which is usually odorless.

3. The roughness of the skin is carried over to the parotoids, which are granulate and warty in the Puna de Atacama toads. In other populations the parotoids are rather smooth, though porous. These glands are rounded in outline except for the subtriangular shape in Vallenar toads.

4. The general ground color of the dorsum is yellowish or olive brown over which irregular large dark spots are usually scattered. The spots are smaller and less frequent in occurrence in the Puna de Atacama, Cordillera Central, and Valdivia toads (Fig. 2). Ventrally all samples are whitish, usually immaculate, or with a few small dark spots. However, the Valdivian toads have a bold, black reticulation covering the entire ventral surface.

5. Juveniles from Paposo and Copiapó are brownish or grayish above with brilliant red color on the tubercles, parotoids, and upper eyelids. Their plantar surfaces are yellow or orange. Juveniles of other populations resemble the corresponding adults.

6. A "hypnotic" defensive reflex similar to that described for *Bufo arenarum* (Cei, 1956 and 1959) occurs in *spinulosus* and varies in frequency of expression as follows: Puna de Atacama, 0 per cent of individuals tested; Paposo 5.2 per cent; Vallenar 22.9 per cent; Santiago 17.2 per cent; Casablanca 66.0 per cent; Cordillera Central 0 per cent. No living Valdivian toads were available.

Discussion

The small, warty toads of Puna de Atacama differ from the populations to the south and southwest in most of the characters listed in Table 1 and in the roughness of the skin. The barrier formed by the great Atacama Desert to the south probably accounts for this differentiation. It is interesting that the Puna de Acama toads do not differ from those from the north (Putre, Chile, and Cuzco, Peru). Either the conditions of selection are much the same from Puna de Atacama to Cuzco, or dispersal is relatively easy in this mountainous area, or both.

The second Chilean group, from the areas of Paposo and Vallenar, are partially isolated by desert from populations to the north and south. They are larger and smoother than Puna de Atacama

toads, but not so large as those from central Chile. In general, they are intermediate between those two groups of populations and less differentiated than Puna de Atacama toads.

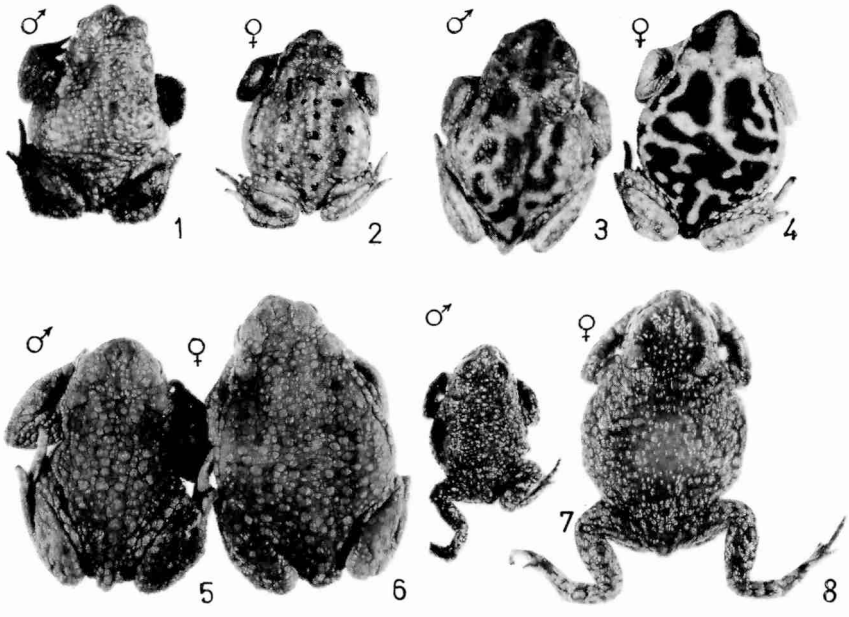

Fig. 2. Dorsal views of male and female specimens of *Bufo spinulosus* from the four geographic groups studied: 1-2 Puna de Atacama, 3-4 Atacama Desert, 5-6 Central population (Cordillera), 7-8 Valdivia.

The central Chilean populations, from Santiago, Casablanca, Cordillera Central, Valparaiso, and Coquimbo, attain the largest size of any Chilean toads. Their legs are somewhat shorter than those of toads to the north.

The fourth group of populations, from the Valdivian rainforest, is the only one in Chile occupying a truly humid zone. Next to the Puna de Atacama group, these toads are the most differentiated of the Chilean populations. The small size and the boldly marked venter are especially conspicuous. A related species, *Bufo variegatus* (Günther), is sympatric with *spinulosus* in this southern forest region.

Local differentiation among the Chilean populations of *spinulosus* are most pronounced at the extreme north and south. In the north, the desert, a barrier to dispersal, presumably has permitted Puna de Atacama toads to acquire local characteristics. In the south

Table 1. Statistically significant (+) difference between samples of *Bufo spinulosus* in characters of Table 1.

Populations	Sex	Snout-vent	Head shape	Hind leg	Fore leg	Interorbital	Nostril position	Snout: Interorbital	Parotoid	Total sig. diff.
Puna de Atacama — Paposo	♂	+	o	+	+	+	+	+	+	7
	♀	+	o	+	+	+	o	+	o	5
— Vallenar	♂	+	+	+	+	+	+	+	o	7
— Santiago	♂	+	+	+	+	+	+	+	+	8
	♀	+	+	+	+	+	+	+	o	7
— Cordillera	♂	+	+	o	o	+	+	+	o	5
	♀	+	o	o	+	+	+	+	o	5
— Casablanca	♀	+	o	o	+	+	+	+	o	5
— Valdivia	♂	+	o	o	+	+	+	+	+	6
	♀	o	o	+	+	+	o	+	+	5
Paposo — Vallenar	♂	o	o	+	o	+	o	o	o	2
— Santiago	♂	+	o	o	+	+	+	o	o	4
	♀	o	o	o	o	o	o	o	o	0
— Cordillera	♂	+	+	+	o	o	o	o	o	3
	♀	o	o	+	o	o	+	o	o	2
— Casablanca	♀	+	o	+	o	o	+	o	o	3
— Valdivia	♂	+	+	+	+	+	o	o	o	5
	♀	+	o	o	o	o	+	o	o	2
Vallenar — Santiago	♂	+	o	+	+	+	+	o	o	5
— Cordillera	♂	+	+	+	o	+	o	o	o	4
— Valdivia	♂	+	+	o	+	+	o	+	o	5
Santiago — Casablanca	♀	o	+	o	o	o	o	o	o	1
— Cordillera	♂	+	+	+	+	+	o	o	o	5
	♀	o	+	+	+	o	o	o	o	3
— Valdivia	♂	+	+	+	o	+	+	+	o	6
	♀	+	o	o	o	o	+	o	o	2
Casablanca — Cordillera	♀	o	o	o	o	+	o	o	o	1
Cordillera — Valdivia	♂	+	+	o	+	o	o	o	+	4
	♀	+	o	+	o	o	+	o	o	3
Casablanca — Valdivia	♀	+	o	o	o	o	+	o	o	2

no such barrier exists, but the radically different conditions of selection to be found in humid forest as compared to steppes may account for the differentiation of the Valdivian toads. Supporting the last suggestion is the striking morphological parallelism of Valdivian *Bufo variegatus* with the local population of *B. spinulosus*.

Brown (1957) has called attention to a common phenomenon of speciation in which distinct races and daughter species accumulate at the periphery of the range of a species. Brown designates this phenomenon "centrifugal speciation" because he considers the center or main body of the species population to be the principal source of evolutionary change and suggests that variants radiate from the center to become isolated or semi-isolated at the periphery during unfavorable periods of range contraction. *Bufo spinulosus* and its relatives may be a case in point. A similar interpretation of geographic variation can be applied to another widespread Chilean species. *Pleurodema bibroni* (Cei, 1959a), and to the occurrence of oviducts in male *Rana pipiens* (Moore, 1944).

As we have just seen, local differentiation of *spinulosus* is best developed at the extreme north and south of its range in Chile. Vellard (1956) suggests that *Bufo trifolium* or *cophotis* in the north and *Bufo variegatus* in the south occur with *spinulosus* as distinct but closely related species. If *cophotis* and *variegatus* are in fact derived from an ancient *spinulosus*-like stock, they represent earlier waves of emigration from the center of the range and have developed isolating mechanisms while in these peripheral situations. When subsequent waves of emigration reached these areas, hybridization either was restricted or did not occur because isolating mechanisms had developed in the intervening time. The types of *spinulosus* characteristic of the Puna de Atacama and the Valdivia populations represent these later emigrations, and presumably are themselves now acquiring the characters leading to reproductive isolation.

Summary

Analysis of geographic variation shows that populations of *Bufo spinulosus* Wiegmann are differentiated in Chile. Four recognizable, though broadly intergrading, population groups are indicated, corresponding to: (1) the northern mountainous arid environment of the Pune de Atacama plateau; (2) the isolated valleys and streams of the desert area of Atacama; (3) the central area between Coquimbo and Angol; and (4) the southern, humid Valdivian Forest.

Polymorphism was observed in some characters and clinal tendencies in others.

Acknowledgments

I wish to thank Dr. R. F. Inger of the Chicago Natural History Museum and Dr. Rodolfo Ruibal of the University of California,

Riverside, for their very valuable criticism and help. I am also indebted to the late Dr. K. P. Schmidt for many friendly suggestions.

LITERATURE CITED

Boulenger, G. A. 1882. Catalogue of the Batrachia Salientia Ecaudata in the collection of the British Museum. Taylor and Francis, London. xvi+495 pp., 30 pls.

Brown, W. L. 1957. Centrifugal speciation. Quart. Rev. Biol., 32:247-277.

Cei, J. M. 1956. Observaciones geneticas preliminares en poblaciones de Anfiobios argentinos. Biologica, 22:45-49.

———— 1958. Polimorfismo y distribución geografica de *Pleurodema bibroni*. Invest. Zool. Chil., *4*:300-327.

———— 1959. Ecological and physiological observations in polymorphic populations of *Bufo arenarum* from Argentina. Evolution *13*:532-536.

Fisher, R. A. and F. Yates. 1948. Statistical tables for biological, agricultural and medical research. 3rd ed. Hafner Publ. Co., New York viii+112 pp.

Inger, R. F. 1954. Systematics and zoogeography of Philippine Amphibia. Fieldiana, Zool., 33:183-531.

Moore, J. A. 1944. Geographic variation in *Rana pipiens* Schreiber of eastern North America. Bull. Amer. Mus. Nat. Hist., 82:349-369.

Vellard, J. 1956. Répartition des batraciens dans les Andes au sud de l'equateur. Trav. Inst. Franc. d'Etudes Andines, 5:141-161.

———— 1959. Estudios sobre batracios andinos. V. El genero *Bufo*. Mem Mus. Hist. Nat. Xavier Prado, 8:1-48, 14 pls.

Wiegmann, A. F. A. 1834. Beiträge zur Zoologie . . . Reise um die Erde, von Dr. F. J. F. Meyen. Amphibien, :185-268, 10 pls.

INSTITUTO DE BIOLOGIA
FACULTAD DE CIENCIAS MERICAS
UNIVERSIDAD NACIONAL DE CUYO
MENDOZA, ARGENTINA